8-2007

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Mark A. Colwell
Humboldt State University

Susan J. Hurley
Humboldt State University

James N. Hall
Humboldt State University

Stephen J. Dinsmore
Iowa State University, cootjr@iastate.edu

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The Condor 109:638–647

AGE-RELATED SURVIVAL AND BEHAVIOR OF SNOWY PLOVER CHICKS

MARK A. COLWELL[1,3], SUSAN J. HURLEY[1], JAMES N. HALL[1], AND STEPHEN J. DINSMORE[2]

[1]*Department of Wildlife, Humboldt State University, Arcata, CA 95521*
[2]*Department of Natural Resource Ecology and Management, Iowa State University, Ames, IA 50011*

Abstract. Precocial young often experience high mortality prior to achieving flight, especially in the first days after hatching. We quantified relationships between chick age, survival, behavior, and response to natural and anthropogenic danger for the threatened Western Snowy Plover (*Charadrius alexandrinus nivosus*) in coastal northern California, USA. Plover chicks were most likely to die in the first three days of their 28-day prefledging period, especially on sandy ocean beaches compared to coarser substrates of river habitats. Chick survival in both habitats increased across the ~120-day chick-rearing period. Improved survival of older chicks coincided with an age-related reduction in brooding and increased distance from the tending parent, which was not related to season. Lower survival of younger chicks was correlated with a tendency to lie motionless when approached by humans; nearly all older chicks responded to human approach by running to evade danger. Chicks of all ages were more likely to lie motionless when potential avian predators flew nearby. Age-dependent survival of Snowy Plover chicks paralleled a trend of increasing development, thermal independence from adults, and capability of evading predators.

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Supervivencia Relativa a la Edad y Comportamiento de los Pichones de *Charadrius alexandrinus*

Resumen. Los pichones precociales usualmente experimentan una alta mortalidad antes de adquirir la capacidad del vuelo, especialmente en los primeros días luego de eclosionar. Cuantificamos la relación entre la edad del pichón, la supervivencia, el comportamiento y la respuesta a peligros naturales y antropogénicos para la especie amenazada *Charadrius alexandrinus nivosus* en el área costera del norte de California, EUA. Los pichones de *C. a. nivosus* presentaron mayor probabilidad de morir durante los primeros tres días del período de 28 días que antecede al emplumamiento, especialmente en las playas de arena del océano comparadas con los substratos más rugosos de los ambientes ribereños. La supervivencia de los pichones en ambos ambientes incrementó a lo largo de los ~120 días del período de cría de los pichones. La mejora en la supervivencia de los pichones de mayor edad coincidió con una reducción de la nidada dependiente de la edad y con un incremento de la distancia entre los polluelos y el progenitor a cargo, lo cuál no estuvo relacionado con la estación. La supervivencia más baja de los pichones más jóvenes estuvo correlacionada con una tendencia a permanecer inmóvil con el acercamiento de los humanos; casi todos los pichones de mayor edad huyeron corriendo de los humanos para evadir el peligro cuando éstos se les acercaron. Los pichones de todas las edades tuvieron una mayor probabilidad de permanecer inmóviles cuando las aves depredadoras potenciales volaron cerca de ellos. La supervivencia dependiente de la edad de *C. alexandrinus* se expresa en forma paralela con la tendencia a un mayor desarrollo, la independencia térmica de los adultos y la capacidad de evadir a los depredadores.

INTRODUCTION

Precocial birds (e.g., shorebirds) hatch from energy-rich eggs in a well-developed state. After leaving the nest, chicks are tended by parents for varying periods, during which time they become increasingly independent. As they age, chicks become more proficient at thermoregulating (Visser and Ricklefs 1993, Schekkermann and Visser 2001, Schekkermann et al. 2003), foraging (Kersten and Brenninkmeijer 1995), and evading predators (Powell 1992). A consequence of this increasing independence is a tendency for chick survival to increase with age.

Manuscript received 22 August 2006; accepted 25 April 2007.
[3] E-mail: mac3@humboldt.edu

TABLE 1. Age at fledging, estimates of chick survival, and characteristics of mortality for selected precocial species.

Species	Fledging age (days)	Proportion of young fledged	Mortality			Source
			Timing (days)	Total (%)	Primary cause	
Brant (*Branta bernicla*)	40–50	0.56–0.79	1–15	>82	Predation	Flint et al. (1995)
Wood Duck (*Aix sponsa*)	56–70	0.41	1–14	86	Unknown	Ball et al. (1975)
Mallard (*Anas platyrhynchos*)	42–60	0.40	1–18	87	Unknown	Orthmeyer and Ball (1990)
Lesser Scaup (*Aythya affinis*)	45–50	–	1–10	94	Not reported	Corcoran et al. (2007)
Snowy Plover (*Charadrius alexandrinus*)	27–31	0.39–0.42	1–6	70	Predation	Warriner et al. (1986)
		0.11–0.76	1–10	83	Predation	Colwell et al. (2005)
Common Ringed Plover (*C. hiaticula*)	20	0.40–0.60	1–7	100	Predation	Pienkowski (1984)
Piping Plover (*C. melodus*)	20–32	0.33	1–10	55	Predation	Loegering and Fraser (1995)
		0.36	1–7	100	Predation	Powell (1992)
Killdeer (*C. vociferus*)	25	0.27	1–7	76	Predation	Powell (1992)
Western Sandpiper (*Calidris mauri*)	16	–	1–5	–	Not reported	Ruthrauff and McCaffery (2005)

Age-dependent survival parallels the changing behaviors of developing young. Early on, chicks are less mobile, often aggregate near siblings when brooded, and respond to danger by lying motionless; as they age, chicks spend more time at greater distances from parents and siblings, and tend to move away from danger. Ruthrauff and McCaffery (2005) suggested that these patterns of behavior and spacing were the cause of age-dependent survival patterns in young Western Sandpipers (*Calidris mauri*). Data from other precocial species suggest a common pattern of high mortality early in life, with a principal cause being predation (Table 1).

The Western Snowy Plover (*Charadrius alexandrinus nivosus*) is a threatened shorebird that breeds along the Pacific coast of North America (U.S. Fish and Wildlife Service 1993), where its population occurs in habitats highly valued by humans. The species' recovery plan (U.S. Fish and Wildlife Service 2001) identifies three limiting factors—human disturbance, predation of eggs and chicks, and degradation of breeding habitat by introduced plants—as causes of the species' population decline. Each of these limiting factors acts to decrease breeding productivity by compromising nesting or fledging success. Along the Pacific coast, plovers breed over nearly six months, with the first clutches initiated in March and the last chicks fledged in September (Page et al. 1995). Pairs share incubation for approximately 28 days, after which males typically care for chicks for another 28 days (Page et al. 1995). In coastal northern California, plovers breed on ocean beaches and riverine gravel bars, two distinct habitats that differ in quality as gauged by per capita reproductive success (Colwell et al. 2005). The long breeding season and extended parental care afford a unique opportunity to examine survival of Snowy Plover chicks while incorporating effects of season and habitat. Here, we quantify age-dependent survival of Snowy Plover chicks and discuss patterns in relation to age-related changes in brooding behavior and distance from the tending parent. We conclude with conservation implications.

METHODS

STUDY AREA

We studied plovers in coastal northern California for four years (2001–2004) at multiple locations in two habitat types, ocean beaches and riverine gravel bars (see Colwell et al. [2005] for a map and detailed site descriptions). On

TABLE 2. Annual variation in the number of Snowy Plover broods and chicks sampled in river and beach habitats of coastal northern California, 2001–2004.

	Beach		River		Total	
Year	Broods	Chicks	Broods	Chicks	Broods	Chicks
2001	11	29	20	49	31	78
2002	11	27	14	37	25	64
2003	12	27	14	33	26	60
2004	17	37	11	25	28	62
Total	51	120	59	144	110	264

beaches, plovers bred on sandy substrates in sparse debris fields consisting of decomposing brown algae (e.g., *Fucus*, *Egregia*, and *Postelsia* spp.), dried invertebrates (e.g., *Velella* spp.), decapod carapaces, bivalve shells, small woody debris, and sparse vegetation. At most beach locations, European dune grass (*Ammophila arenaria*), an introduced species, occurred in dense stands. Gravel bars were located along the lower Eel River, approximately 15 km upstream from its confluence with the Pacific Ocean. On gravel bars, plovers bred on coarse substrates sparsely vegetated by willow (*Salix* spp.) and white sweet clover (*Melilotus alba*). We commonly used plover tracks on the sandy beaches to find nests and track broods; this was rarely the case in coarse substrates along the river. Beaches had significantly higher levels of human activity than gravel bars (Colwell et al. 2005).

FIELD OBSERVATIONS

We monitored plovers from 15 March until early September, when the last chicks fledged. We marked adult plovers with a unique combination of colored bands, and we banded chicks at hatching with a metal (U.S. Fish and Wildlife Service) band wrapped with brood-specific colored tape to distinguish chicks of similar age raised in a common area. To quantify chick survival, we checked broods at 1–4 day intervals for 28 days, the age at which young fledge (Page et al. 1995). We monitored 264 chicks in 110 broods over the four years of study (Table 2), which represented nearly all known chicks in coastal northern California (Colwell et al. 2005).

When monitoring broods, we recorded locations, identified tending adult(s), and noted the number of chicks. In 2003 and 2004, we sampled chick behaviors during 15-min focal observations (Altmann 1974), initiated at distances of >100 m and after a 5-min wait to minimize disturbance. At 30 sec intervals, we recorded chick behavior as: 1) brooding, when a chick crouched under a parent's wing or brood patch; 2) feeding, when they searched for, pursued, or handled prey; 3) disturbed, when chicks remained crouched and motionless or ran away from danger; or 4) other, which included preening or loafing. At minute intervals, we categorized the distance of each chick from its parent as: brooding under the parent (0), ≤1 m (1), 1–10 m (2), 10–50 m (3), 50–100 m (4), or >100 m (5). For each focal observation, we averaged behaviors and distances for all chicks tended by one adult to yield an estimate for each brood of a given age, which was the unit observation in behavioral analyses (see below). Our sample was a subset of the broods used in the survival analysis, consisting of 2003 and 2004 broods sampled unevenly across habitats and dates. Therefore, we were unable to directly relate chick survival to behavior.

To quantify response to a mammalian predator (simulated by a human), we approached broods at the end of a focal observation by walking directly toward them at a constant speed. Using a handheld global positioning system, we recorded our initial observation site, where chicks reacted to our approach, and the location we first observed the brood. We categorized the reaction of chicks to our approach as either: 1) lie motionless, or 2) run, in which a chick moved steadily away from the disturbance. During focal observations, we opportunistically recorded behavioral responses to natural disturbances.

DATA SUMMARY AND ANALYSIS

We used an information-theoretic approach (Burnham and Anderson 2002) to understand

how habitat, year, season, and chick age influenced the survival of dependent Snowy Plover chicks.

Habitat and year. Nests occurred in two distinct habitats, coastal beaches (beach) and along the gravelly shores of the Eel River near the coast (river), which differed in fledging success (Colwell et al. 2005). Annual effects were of interest because we knew from previous work (Colwell et al. 2005) that nest and chick survival varied annually, so we included a year effect in our set of candidate models.

Season. In our study area, plovers bred over six months, with the first eggs laid in mid-March, the first chicks hatching in early May, and the last chicks fledging in early September. During this interval chicks may be exposed to a range of weather conditions and variation in human disturbance and danger of predation. To account for this variation, we fitted simple models in which survival was allowed to exhibit a linear or quadratic trend across the four-month chick-rearing season. Such variation in chick survival has been found for other shorebirds (Knopf and Rupert 1996, Wolcott and Wolcott 1999, Ruthrauff and McCaffery 2005).

Age. In other shorebirds (Graul 1973, Ruthrauff and McCaffery 2005, Morse et al. 2006), there is evidence that chick survival during the first few days of life is low (Table 1). To account for this, we examined four models summarizing a range of short-term effects on chick survival. We used four intervals, representing 3-, 5-, 7-, and 10-day effects beginning at hatching, to capture what we believed to be short-term reductions in chick survival. Although we believed that plover chick survival changed rapidly during the first 10 days, we had no a priori reason to believe it was an interval of specific length. Thus, this range of intervals encompassed a range of days post-hatching during which we believed most mortality occurred.

We modelled chick survival using the nest survival model (Dinsmore et al. 2002) in Program MARK (White and Burnham 1999). This model is similar to Kaplan-Meier models typically used for analyses of radio-telemetry data (Pollock et al. 1989), although it does not require knowledge of an exact failure date. Although Lukacs et al. (2004) recently developed a method for estimating chick survival when individual birds are not marked, this approach requires that the number of sampling occasions is fixed. In our study, we did not mark individual chicks with unique band combinations, but tending adults were individually color-banded. We monitored broods intensively and, because broods occupied open habitats where we could easily observe chicks, we assumed that we observed all living chicks during each survey. Indeed, in only two cases did the number of chicks in a brood increase on a subsequent brood check. We were, therefore, confident in our ability to detect all chicks in a brood on each visit. Consequently, we assumed chick fates were known with certainty on each check, monitored broods at irregular (1–4 day) intervals, and chose the nest survival model in Program MARK to investigate chick survival in favor of other approaches (Lukacs et al. 2004, Ruthrauff and McCaffery 2005).

We used an information-theoretic approach to model selection (Burnham and Anderson 2002). We ranked our set of candidate models using Akaike's information criterion (AIC; Akaike 1973) corrected for small sample sizes (AIC_c). To compare competing models, we used ΔAIC_c values and computed normalized weights (w_i) to provide a measure of the relative support for each model. When examining specific model effects (e.g., covariates), we present beta parameter estimates and 95% confidence intervals, and infer strong effects as those in which confidence intervals do not include zero. We averaged parameter estimates across all candidate models to obtain the best estimate(s) of chick survival accounting for model selection uncertainty (Burnham and Anderson 2002). We approached modelling in a hierarchical, three-step manner. First, we fit the following models to explain seasonal variation in chick survival: 1) a linear trend, 2) a quadratic trend, 3) models to explain short-term effects at 3-, 5-, 7-, and 10-day intervals, and 4) a model with no seasonal effects. We decided a priori that we would move forward with effects that were competitive (ΔAIC_c values <2). In the second step, we included effects of year and habitat (additively) in the best model(s) from step 1. Lastly, we added three models to address specific questions about the influence of year and habitat on chick survival: 1) a model with only habitat; 2) a model with only year effects; and 3) a model in which habitat and year were combined in

TABLE 3. Results of model selection examining factors influencing Snowy Plover chick survival in coastal northern California, 2001–2004. Models are ranked by scaled values of Akaike's information criterion corrected for small sample sizes (ΔAIC_c) and Akaike weights (w_i), which represent support for each model given the data. K is the number of model parameters. All a priori candidate models are shown.

Model effects[a]	Deviance	K	ΔAIC_c[b]	w_i
Year + habitat + linear trend + 3-d	872.43	7	0.00	1.00
3-d	941.33	2	58.88	0.00
Year + habitat + linear trend	936.94	6	62.51	0.00
5-d	946.18	2	63.73	0.00
Year + habitat + quadratic trend	936.39	7	63.96	0.00
10-d	951.95	2	69.50	0.00
7-d	953.45	2	71.00	0.00
Year * habitat	951.59	8	81.17	0.00
Year + habitat	957.83	5	81.39	0.00
Habitat	987.69	2	105.24	0.00
Year	1018.19	4	139.74	0.00
Linear trend	1030.68	2	148.23	0.00
Quadratic trend	1030.65	3	150.20	0.00
No effects (null model)	1039.05	1	154.60	0.00

[a] Model effects are as follows: habitat = river vs. beach; linear and quadratic trend relate to effects of season (date); and 3-, 5-, 7-, and 10-d represent short-term effects of chick age (days).
[b] The AIC_c score for the top model was 886.45.

a multiplicative fashion. We assessed the fit of the survival model to our chick survival data using a chi-square test of independence of the fates of chicks within broods as a function of brood size (Dinsmore and Knopf, in press).

We analyzed age-related changes in chick behavior using linear regression, with days since hatching as the predictor variable and percentage of time being brooded, average duration (min) of brooding bouts, and distance (m) from the tending adult as response variables. We used ANCOVA to examine relationships among behavioral variables and effects of year, habitat, and brood survival (fledged vs. died), with age (days since hatching) and season (date) as covariates. We used logistic regression to examine age-related responses of chicks to human approach, with days since hatching as the predictor variable and behavior (motionless vs. evasive) as the response variable. We examined interactions between response and year, habitat, and success with each of these variables as the predictor. We used a Mann-Whitney U-test to compare the ages of chicks that either lay motionless or ran in response to human approach and natural occurrences of avian predators. We present means with 95% confidence intervals for survival estimates or ± SD for behavioral data.

RESULTS

CHICK SURVIVAL

From 2001 to 2004, we monitored 264 plover chicks in 110 broods over 124 days from 9 May to 9 September. There was a significant lack of fit of the chick survival model to our data ($\chi^2_8 = 44.5$, $P < 0.01$). However, most (52%) of this lack of fit was due to a greater than expected number of complete losses of three-chick broods; there was no similar pattern of complete losses among two-chick broods. Because remaining test components balanced contributions to the overall test statistic, we proceeded with the analysis.

Model selection results showed that a model with additive effects of year, habitat, seasonal variation, and a three-day short-term effect strongly influenced chick survival (Table 3). This model received all the support. Parameter estimates from this best model showed that chick survival was highest in 2001 and 2004, and substantially lower in intervening years. The habitat effect in the best model indicated that chicks survived poorly in beach compared to river habitats ($\hat{\beta}_{beach} = -1.55$, 95% CI: -1.93, -1.17 on a logit scale). Survival over the season was best explained by a linear trend ($\hat{\beta}_{Linear} = 0.16$, 95% CI: 0.09, 0.23 on a logit

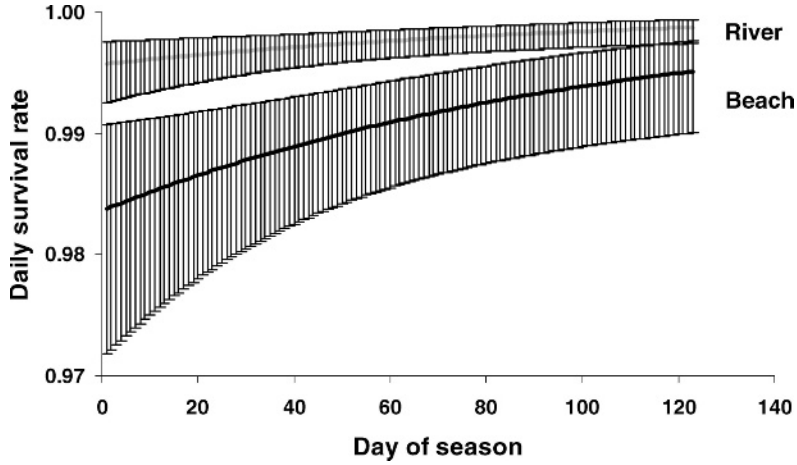

FIGURE 1. Snowy Plover chicks raised in river habitats had higher daily survival rates than chicks reared on beaches in coastal northern California. Daily survival rates were predicted using the best model selected using Akaike's information criterion (Table 3), and are shown with 95% confidence intervals. Day 1 of the chick-rearing season corresponds to 9 May.

scale). Lastly, chicks less than three days old had a significantly higher mortality rate than older chicks. Predicted fledgling period survival along the river ranged from 0.47 (95% CI: 0.30, 0.62) in 2002 to 0.80 (95% CI: 0.69, 0.87) in 2001, whereas survival of beach-reared chicks was much lower and ranged from 0.06 (95% CI: 0.02, 0.17) in 2002 to 0.42 (95% CI: 0.25, 0.58) in 2001. To illustrate the effects of seasonal variation and habitat on survival, we plotted predicted daily chick survival rates from our best model for 2001 (Fig. 1).

BEHAVIOR OF CHICKS

Age-related behaviors of chicks indicated a pattern of growing independence from adults (Fig. 2), and these patterns were unrelated to season (all $P > 0.12$). As chicks aged, they were brooded less ($R^2 = 0.57$, $P < 0.001$) and for shorter durations ($R^2 = 0.12$, $P < 0.001$), and their distances from the tending parent increased ($R^2 = 0.49$, $P < 0.001$). Overall, chicks were brooded an average of 38% of the time across all ages and habitats. Chicks 10 days of age or younger were brooded an average of 58% ± 25% of the time compared with 17% ± 24% for older chicks. At a given age, the amount of time chicks were brooded did not differ between years ($F_{1,285} = 0.4$, $P = 0.51$) or habitats ($F_{1,285} = 0.4$, $P = 0.51$).

Survival of chicks was correlated with brooding behavior. Overall, chicks that fledged were brooded less on average (35% ± 2%) than those that did not survive (69% ± 5%; $F_{1,285} = 6.3$, $P = 0.01$). This pattern was true for beach-reared chicks ($F_{1,100} = 4.9$, $P = 0.03$), but not those raised along the river ($F_{1,184} = 0.1$, $P = 0.82$). At a given age, distance between chicks and their tending parent did not differ between years ($F_{1,280} = 0.1$, $P = 0.93$) or habitats ($F_{1,280} = 3.4$, $P = 0.07$). Distance between chicks and their parent did not differ between broods that failed or fledged ($F_{1,280} = 0.6$, $P = 0.46$).

The behavior of chicks approached by humans changed abruptly with age. By 10 days of age, there was a 90% chance that chicks approached by a human would run away ($\hat{\beta} = 0.37 \pm 0.07$ SE, $\chi^2 = 82.3$, $P < 0.001$). This behavior was consistent between years ($\chi^2 = 0.4$, $P = 0.55$) and between habitats ($\chi^2 = 0.1$, $P = 0.94$). Viewed another way, chicks that remained motionless were significantly younger (3.4 ± 3.0 days) than those that ran from approaching humans (14.6 ± 7.9 days). There was no difference in response to human approach for broods that fledged at least one chick compared with broods that failed ($\chi^2 = 0.05$, $P = 0.85$).

Chicks responded differently to avian predators compared to humans. Nearly all (33 of 34) chicks lay motionless in response to the approach of a potential avian predator. Moreover, chicks remained motionless at older ages when approached by a bird (7.1 ± 6.7 days)

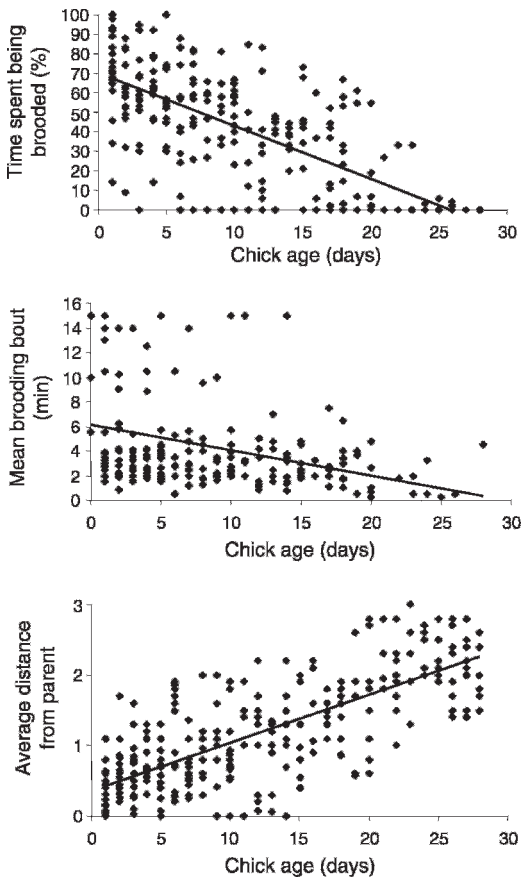

FIGURE 2. As Snowy Plover chicks aged they spent less time being brooded (top), were brooded for shorter durations (middle), and increased their distance from the tending adult (bottom). Distance from the tending adult was categorized as 0 = brooding under parent, 1 = ≤1 m from parent, 2 = 1–10 m from parent, and 3 = 10–50 m from parent.

compared to a human ($z = 2.7$, $P = 0.006$). Potential avian predators that elicited a response included Common Ravens (*Corvus corax*, $n = 20$), American Crows (*C. brachyrhynchos*, $n = 3$), gulls (*Larus* spp., $n = 3$), Caspian Terns (*Sterna caspia*, $n = 3$), Turkey Vultures (*Cathartes aura*, $n = 3$), Double-crested Cormorants (*Phalacrocorax auritus*, $n = 1$), and Canada Geese (*Branta canadensis*, $n = 1$).

DISCUSSION

Several important results emerge from this study. First, age-dependent survival of Snowy Plover chicks paralleled behavioral changes of developing young and their growing independence from parents. Early in life, adults brooded chicks more often and for longer durations, and as a consequence chicks tended to be nearer adults. These patterns, coupled with the tendency for young chicks to remain motionless, contributed to the poor survival of chicks <3 day old. Secondly, despite annual variation, chick survival increased seasonally, which suggests that environmental factors consistently influenced survival. Finally, Snowy Plover chicks survived poorly on ocean beaches compared with river habitats, which elucidates mechanisms leading to differences in habitat quality (Colwell et al. 2005).

AGE-DEPENDENT SURVIVAL

The pattern of increasing survival with chick age is similar to that reported for other precocial species. Among shorebirds and waterfowl, survival is lowest early in life, with 55%–100% of mortality occurring in the first few weeks after hatching (Warriner et al. 1986, Flint et al. 1995). The uniformity of this age-related survival pattern across taxa suggests a common explanation related to development, dependence on adults, and vulnerability to predators.

Comparatively high mortality among young age classes of precocial species correlates with an interval in which chicks are often brooded by adults, and siblings remain in close proximity to one another and their parent(s). Shorebird chicks are dependent on the tending parent for warmth for the first 10 day of life, and progressively less so for up to a week after that (Pienkowski 1984). Piping Plover (*Charadrius melodus*) chicks were not observed being brooded after 14 days of age (Powell 1992), and young Semipalmated Plovers (*Charadrius semipalmatus*) were rarely observed being brooded after five days of age (Blanken and Nol 1998). In this study, some Snowy Plover chicks brooded much longer, up to fledging, which is remarkable given the temperate conditions of our study area. However, prolonged brooding is not unusual (Schekkermann et al. 2003). The length of brooding bouts decreased as chicks aged, and lasted about 4 min on average. In contrast, brooding bouts of European Golden-Plover (*Pluvialis apricaria*) chicks lasted an average of 12 min and did not vary with age (Krijgsveld et al. 2003).

At hatching, shorebird chicks have energy reserves in their residual yolk sac, yet they must be able to feed themselves, balance thermoregulatory needs, and avoid predators. As a result, the mass of chicks, weather conditions, and risk of predation may interact to influence survival. For example, European Golden-Plover chicks that survived the first week of life gained significantly more weight in the first two days of life than their counterparts that died (Pearce-Higgins and Yalden 2002). Heavier Western Sandpiper chicks were more likely to survive their 15-day fledging period than chicks of lower mass (Ruthrauff and McCaffery 2005). We lack data to evaluate the contribution of neonate mass to subsequent survival. However, small reductions in energy intake may slow growth in young chicks (Schekkerman and Visser 2001), making them more dependent on adults. Consequently, shorebird chicks, especially small neonates (Visser and Ricklefs 1993), are probably most vulnerable when disturbed during periods of inclement weather (Schekkerman and Visser 2001), which has consequences for survival.

Brooding itself may increase the danger posed to young chicks by attracting predators. The plumage of adult birds is more visible to potential predators than the cryptic natal down of chicks. An adult surprised by a potential predator often leaves chicks exposed and clustered, and hence vulnerable to predation. Therefore, for young chicks, thermoregulatory stress may lead to increased brooding and greater vulnerability to predation. Frequent and prolonged human disturbance near young chicks could initiate this sequence of events by keeping parents from brooding chicks, thus increasing thermoregulatory costs (Visser and Ricklefs 1993), potentially reducing rates of development (Schekkermann and Visser 2001), and increasing predation risk. Alternatively, the tendency of chicks to run when approached by humans may make them more vulnerable to predation.

Finally, the response of young plovers to danger as simulated by the approach of humans changed abruptly as they aged, and this behavior contrasted with the response to naturally occurring avian predators. Young chicks often remained motionless when approached; by 10 days of age nearly all chicks ran from an approaching human. Page et al. (1995) reported that this behavioral change occurred at 14 days. However, we found that even very young chicks occasionally ran from an approaching human. In contrast, chicks lay motionless in response to flying avian predators in virtually all observed encounters. Age-related variation in the behavioral response of Snowy Plover chicks to different species may relate to speed of approach, type of predator, or whether chicks or tending adults first detect the danger. Even young chicks may be able to evade an approaching human when alerted at a great distance by vocalizations of a tending adult. In contrast, lying motionless in response to a rapidly approaching avian predator may be an effective response.

SEASONAL VARIATION IN SURVIVAL

In both habitats, Snowy Plover chick survival increased over the season. Other studies of shorebirds have demonstrated either a seasonal increase (Morse et al. 2006) or decrease (Ruthrauff and McCaffery 2005) in chick survival. Compared to other North American shorebirds, even those breeding at comparable latitudes (e.g., Spotted Sandpiper [*Actitis macularius*]; Oring et al. 1983), the Pacific coast population of the Snowy Plover has a long breeding season (Warriner et al. 1986). Consequently, plover chicks may hatch over a 4–5 month interval during which inclement weather and predation danger vary greatly. Chicks hatching in early spring may experience cool, wet weather, causing them to be more susceptible to hypothermia when adults cannot effectively brood them; in contrast, late-season chicks that were unattended by adults occasionally survived (MAC, pers. obs.). On beaches, comparatively higher human activity (Colwell et al. 2005) may exacerbate this early season effect (see below). Alternatively, chicks hatching later in summer may be at lower risk of predation when they co-occur with large flocks of southbound migrant sandpipers, which begin to arrive in our study area in late June.

HABITAT PATTERNS

Our findings elucidate the nature and timing of differences in habitat quality between river and beach sites (Colwell et al. 2005). On beaches, we regularly used predator exclosures to increase nesting success (40%), albeit to a level less than

that on the river (53%; Colwell et al. 2005). Given that the average number of chicks hatched per male was similar in the two habitats (beach: 2.7 ± 1.9; river: 2.5 ± 1.7; Colwell et al. 2005), we conclude that low productivity of beach-breeding plovers stems from low chick survival. Elsewhere (Colwell et al. 2005), we speculate on the details of predation as the main cause of habitat differences in breeding productivity of plovers.

Low chick survival on beaches may also be compromised by human activity, which was much higher on beaches than gravel bars (Colwell et al. 2005). Other studies of beach-breeding plovers have reported a negative correlation between human activity and either chick survival (Ruhlen et al. 2003) or reproductive success (Flemming et al. 1988). Human activity may decrease chick survival in several ways. Direct mortality may occur when vehicles or humans crush chicks. For example, Melvin et al. (1994) recorded 14 instances over five years in which off-road vehicles ran over Piping Plover chicks, including in areas where vehicles were prohibited. In our study area, vehicles drove on the waveslope of most beaches year-round during the day. High levels of human activity probably also exacerbate low chick survival on beaches indirectly. Chicks may die because human disturbance hinders normal brooding such that chicks, especially young ones, are vulnerable to hypothermia during inclement weather. We attributed the failure of at least one early-season brood to the prolonged presence of humans at an exclosure during cool, windy weather (MAC, pers. obs.). Our finding that beach-reared chicks that perished were brooded at nearly double the rate of chicks that survived suggests that chick survival was compromised by human activity (Colwell et al. 2005). Additionally, beach-reared chicks may perish at a higher rate because predators cue in on conspicuous brooding adults after prolonged human disturbance.

CONSERVATION IMPLICATIONS

Over the four years of our study, management at beach sites (e.g., erecting predator exclosures around nests and fencing to restrict human access to some breeding habitats) was effective at increasing hatching success in this population. However, we have now shown that significantly lower reproductive success of beach-breeding than river-breeding plovers (Colwell et al. 2005) is a result of low survival of young on beaches, especially when chicks are young and vulnerable. Higher mortality of beach-reared chicks indicates that additional management is necessary to increase productivity and recover the local population of this threatened species. Greater restrictions on human activity in the vicinity of breeding plovers or increased predator control may be warranted.

ACKNOWLEDGMENTS

H. Beeler, A. Hoffmann, D. LeValley, R. LeValley, S. McAllister, J. Meyer, C. Millett, Z. Nelson, K. Ross, R. Smith, A. Transou, and C. Wilson provided field assistance on many occasions; many other volunteers and individuals from state and federal agencies also assisted us. We are grateful to J. Watkins for supporting our efforts. We thank several anonymous reviewers for helpful comments. Our work was funded by California Department of Fish and Game, California Department of Parks and Recreation, Chevron Oil Corporation, Eureka Rotary, Humboldt County Fish and Game Advisory Commission, Humboldt County Planning Department, Humboldt State University, Mad River Biologists, Marin Rod and Gun Club, MRB Research, Inc., Redwood Region Audubon Society, Stockton Sportsmen's Club, Western Section of The Wildlife Society, U.S. Bureau of Land Management, U.S. Fish and Wildlife Service, and California Department of Fish and Game's Oil Spill Response Trust Fund through the Oiled Wildlife Care Network at the Wildlife Health Center, School of Veterinary Medicine, University of California, Davis.

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